New Phytologist

Review

Tansley review

Plant science in forest canopies – the first 30 years of advances and challenges (1980–2010)

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Received: *31 October 2011*
Accepted: *5 January 2012*

Contents

New Phytologist (2012)
doi: 10.1111/j.1469-8137.2012.04076.x

Key words: biodiversity, canopy, canopy access, conservation, forest science, science education.

Summary

As an emerging subdiscipline of forest biology, canopy science has undergone a transition from observational, 'oh-wow' exploration to a more hypothesis-driven, experimental arena for rigorous field biology. Although efforts to explore forest canopies have occurred for a century, the new tools to access the treetops during the past 30 yr facilitated not only widespread exploration but also new discoveries about the complexity and global effects of this so-called 'eighth continent of the planet'. The forest canopy is the engine that fixes solar energy in carbohydrates to power interactions among forest components that, in turn, affect regional and global climate, biogeochemical cycling and ecosystem services. Climate change, biodiversity conservation, fresh water conservation, ecosystem productivity, and carbon sequestration represent important components of forest research that benefit from access to the canopy for rigorous study. Although some canopy variables can be observed or measured from the ground, vertical and horizontal variation in environmental conditions and processes within the canopy that determine canopy–atmosphere and canopy–forest floor interactions are best measured within the canopy. Canopy science has matured into a cutting-edge subset of forest research, and the treetops also serve as social and economic drivers for sustainable communities, fostering science education and ecotourism. This interdisciplinary context of forest canopy science has inspired innovative new approaches to environmental stewardship, involving diverse stakeholders.

I. Introduction

In Papua New Guinea, a tribe called the Korowai still lives in the treetops, erecting amazing aerial houses accessible by twig ladders. It is speculated that their unusual habit of community tree houses evolved as a mechanism to escape enemies on the forest floor, and provide a healthy environment above the dank, dark understory. Throughout human history, trees represented safe havens from danger, sites of spiritual connection, and an important source of food, medicines, materials, and productivity (reviewed in Lowman & Rinker, 2004). Although soil and streams provide important childhood 'playgrounds', tree houses remain a foremost recreational vestige of children and adults alike that inspires links between humans and the natural world (Lowman, 2009a; Louv, 2011). Many famous people have played in childhood tree houses – John Lennon (of the Beatles), Winston Churchill, the Roman Emperor Caligula, and Queen Victoria when she was a young princess. Recent medical findings indicate that children who play outdoors and learn about nature have better health and well-being (Louv, 2011).

In an evolutionary sense, humans descended from ancestors in the treetops. Recent findings about ancient hominoids in Ethiopia indicate that our ancestors inhabited forests (not savannahs as previously thought) (White *et al.*, 2009). Why do the treetops continue to hold such spiritual as well as scientific importance for cultures around the world? And why have scientists only recently explored these heights for scientific discovery, given the fact that forestry is a relatively well-established discipline? Only in the past three decades have methods been developed that foster safe, versatile access to the treetops. And even more recently, with the advent of ecosystem services provided by forests gaining traction on the accounting ledgers of policy-makers, forest canopy research has gained attention as forest health links directly to human health (Perrings *et al.*, 2010). Ecosystem services include fresh water yield, genetic libraries, carbon storage, energy production, medicines, food, shade, building materials, soil conservation, and spiritual/cultural heritage. Access to forest canopies has emerged as an important component of whole-forest research, especially with regard to climate change, biodiversity, and ecosystem service analyses (reviewed in Ozanne *et al.*, 2003).

Forest ecosystems are composed of two fundamental subsystems: the forest floor/rhizosphere and the canopy. The canopy is composed of the foliated portion of the forest that represents the photosynthetic engine that captures solar energy and pulls water upward from the soil for exchange with the atmosphere, processes fundamental to sustainability of forest ecosystems and the services they provide. Because the forest floor is relatively easy to access, forest floor communities and processes related to decomposition, water infiltration, aggregate formation and nutrient turnover to roots or export have been studied in forests around the globe for at least two centuries (Coleman *et al.*, 2004). By contrast, the canopy remained a virtual frontier as a result of limited access until relatively recently (Denison *et al.*, 1972; Mitchell, 1982; Perry, 1986). Before the 1970s, canopy research was largely restricted to observations from the ground, from short trees or harvested sites, or from a point in the canopy that could be accessed with ladders (e.g. Beebe, 1949). With the advent of single-rope climbing techniques in the 1970s, followed by towers, balloons and cranes, canopy research in the past 30 yr has advanced by leaps and bounds in understanding of the diversity of canopy organisms and habitats and their effects on primary productivity as this affects local and regional climate and exchange of materials with the forest floor (e.g. Lerdau & Throop, 1999; Novotný *et al.*, 2003; Koch *et al.*, 2004; Lowman & Rinker, 2004).

With their billions of green leaves, the treetops are epicenters of life and the basis of food chains around the planet. Forest canopies reputedly house *c.* 50% of the biodiversity of terrestrial ecosystems (reviewed in Wilson, 1992; May, 2010; Lowman *et al.*, 2012). The combination of sun, fruits, flowers and year-round productivity in tropical rain forests provides ideal conditions for an enormous array of canopy inhabitants. Thousands of species of trees and vines produce a veritable salad bar for millions of insects that in turn are eaten by myriad reptiles, birds, and mammals (Lowman, 1999). Individual bromeliad tanks can house hundreds of residents, many unclassified for science (Lowman *et al.*, 2006). This diversity of organisms is not without influence on the processes of primary productivity, evapotranspiration and exchange of materials among canopy, atmosphere and forest floor. For example, the forest canopy is the interface between 90% of Earth's terrestrial biomass and the atmosphere (Ozanne *et al.*, 2003) and regulates regional and global gradients in temperature, precipitation and airflow (Raupach *et al.*, 1996; Finnigan, 2000; Foley *et al.*, 2003; Juang *et al.*, 2007; Janssen *et al.*, 2008). Anthropogenic activities, as well as natural environmental changes, can alter both diversity and processes in forest canopies that affect regional and global climate, as well as critical ecosystem services. Increasingly, forest canopy scientists – along with coral reef ecologists, soil biologists, ice physicists, water chemists and others – have taken on the role of planetary physicians, working against a nearly impossible timeline to unravel the critical mysteries of how ecosystems function. With access into forest canopies, scientists have demystified some of their complex machinery, but many unanswered questions remain. Advances in forest canopy research during the past 30 yr and future questions comprise the topics of this review.

II. History of canopy access

Early foresters and naturalists based their ideas about forests on observations made at ground level (reviewed in Lowman, 2009a,b). Explorers such as Alfred R. Wallace and Charles Darwin wrote enthusiastically about the unbroken canopy overhead during the late 1800s, and ideas about forest canopies changed very little until almost 100 yr later when a steel tower was installed in Mpanga Forest Reserve, Uganda to monitor insect vectors of human diseases (Haddow *et al.*, 1961). Several years later, Oxford University's Operation Drake installed a canopy structure in the Asian tropics (Mitchell, 1982); ladders were used to study the chromosomal cytology of Himalayan trees (Mehra & Bawa, 1968); a canopy structure in Malaysia was tethered to tree crowns for phenological observations (Muul & Liat, 1970); and a few rigs were installed in Sulawasi forest canopies (Sutton, 2001). All of these early forays into the forest canopy were primarily for purposes of observation and exploration, without long-term viability.

The 1980s was hailed the 'golden age of canopy access' with the development of single rope techniques (SRTs) in the early 1970s (Denison *et al.*, 1972), independently adapted from caving to treetops by Lowman (1984) in Australia and by Perry (1986) in Costa Rica (Fig. 1). Whereas SCUBA equipment in the 1950s

Fig. 1 Single rope techniques (SRTs) represented one of the first, and most affordable, canopy access techniques, as illustrated here by Indian graduate students training to study pollinators.

heralded the age of exploration for coral reefs (reviewed in Sale, 2002), the versatile toolkit of ropes, harness, and climbing hardware enabled scientists to reach the mid-canopy with ease, safely suspended from a rope, to study the diversity of canopy organisms and their roles in the canopy (reviewed in Lowman & Rinker, 2004). SRT is ineffective, however, for reaching the uppermost canopy and the leafy perimeters of tree crowns, as ropes require looping over sturdy branches located close to the tree trunk. To overcome those shortcomings, new tools were designed to reach the perimeters and uppermost canopy. Ladders (Appanah & Chan, 1981), scaffolds (Mehra & Bawa, 1968), walkways (Lowman & Bouricius, 1995), canopy booms (P. Ashton, pers. comm.), hot air balloons (Hallé & Pascal, 1992), and construction cranes (Parker, 1995) all provided access to slightly different regions of the treetops, and hence enabled researchers to answer different questions.

Fig. 2 Canopy walkways provided access to a team of scientists, students, or ecotourists, illustrated here in the Yunnan Province, China.

From their aerial perches, canopy scientists not only documented extraordinary biodiversity but also sounded the alarm about the consequences of deforestation and degradation for these veritable hotspots of life (e.g. Lowman & Selman, 1983). As a consequence, canopy access methods became important for education and ecotourism, as well as research. Canopy walkways for both research and ecotourism now span the globe, from Costa Rica to China (Fig. 2). The first two canopy walkways were constructed nearly simultaneously in 1985: one in Malaysia by Ilaar Muul anchored in tree crowns, and another in Queensland, Australia supported by telephone poles (see Lowman, 1999). The Australian model was an outcome of Lowman's Earthwatch expeditions, which provided both safe access for her volunteers to collect herbivory data and a revenue stream for ecotourism. Five years later, North America's first canopy walkway was constructed in the Hopkins Forest at Williams College, Massachusetts (Lowman & Bouricius, 1995; Lowman, 1999); and America's first public canopy walkway was erected in Myakka River State Park, Florida in 2000 (Lowman *et al.*, 2006; Lowman, 2009b). In addition to the popularity of canopy walkways around the world (http://www.canopyaccess.com), zip lines provide a thrill-ride through the canopy, further reinforcing the notion that forests – if conserved rather than cleared – provide local livelihoods (Lowman, 2009b).

The French-designed hot-air balloon and inflatable raft, called 'Radeau des Cimes,' was designed to reach the uppermost canopy, and flown for expeditions in French Guinea, Gabon, and Cameroon; components were also deployed in Panama and Australia (Hallé & Pascal, 1990) (Fig. 3). This creative canopy access tool has inspired children and researchers world-wide (reviewed in Hallé & Pascal, 1990). Construction cranes represent the most recent tool for safe canopy access (reviewed in Mitchell *et al.*, 2002). The first crane was erected in Panamanian seasonally dry forest by the Smithsonian Tropical Research Institute (Parker, 1995). Cranes were established in Australia, Switzerland, Germany,

Fig. 3 The canopy raft and hot air balloon not only provided access to the uppermost canopy, but also served as a hook for inspiring children and citizens about science.

Japan, Indonesia, the USA, and Venezuela. For financial reasons, the US crane was recently shut down, and the Venezuela crane was decommissioned because of challenges related to its remote location near the Orinoco River.

Essentially from 1980 to 1995, the toolkit for canopy access was developed by a handful of researchers around the world (reviewed in Lowman & Rinker, 2004). With each method facilitating access to specific regions of forest, and designed for different types of data collection, forest scientists could now conduct rigorous, whole-forest research on both mobile and sessile inhabitants, without restriction to the understory alone.

III. Consequences of whole-tree approaches to forest science

Canopy access tools allowed whole-forest approaches to research that truly changed scientific perspectives on forests, just as tools for soil research have expanded forest science below-ground. Before the advent of canopy biology, most scientists were restricted to studying those portions of the forest that could be viewed at ground level, a veritable tunnel from 0 to 2 m high, usually within arms' reach and typically representing < 5% of a tall, mature forest. Not surprisingly, such limited observations often resulted in erroneous conclusions. Foremost of these new discoveries facilitated by canopy access were the findings about biodiversity of forests; spatial and temporal variability in herbivory among different heights in forest canopies; new findings about canopy cover and productivity inspired by above-canopy tools such as satellite imagery, especially useful for modeling; the variability of forest denizens, such as epiphytes, along elevational gradients; horizontal and vertical differences in leaf traits, including rates of photosynthesis, within forest canopies; spatial and temporal variation among canopy populations; long-term consequences of environmental changes for canopy biodiversity and processes; interactions between canopy and atmosphere that affect vertical and horizontal gradients in microclimate within the canopy and affect regional and global patterns of temperature and precipitation; and interactions between canopy and forest floor that drive water transport and biogeochemical cycling. Perhaps the most important benefit of safe access into forest canopies has been experimental manipulation of canopy architecture and diversity to test hypotheses concerning effects of these variables on primary production, carbon flux, and canopy–atmosphere and canopy–forest floor interactions (e.g. Dial & Roughgarden, 1995; Whelan, 2001; De Souza & Martins, 2005; Lindo & Winchester, 2007; Mooney, 2007; Richardson *et al.*, 2010; Shiels *et al.*, 2010).

Forest canopy access significantly advanced and, in some cases, changed our perceptions about many aspects of forest ecology, and also increased the accuracy of information related to forest processes and biodiversity. Quite simply, biologists could not accurately measure forest dynamics or their interactions with the atmosphere and global climate without gaining access to the upper reaches of the trees. Access to whole trees, instead of just understory, led to discovery of millions of new species, changing our perception of global biodiversity (Winchester, 2006). In large part, this diversity of canopy organisms reflects the diversity of canopy habitats and microclimatic conditions within the canopy, which can only be measured within the canopy (Andrade & Nobel, 1997; Dial *et al.*, 2004; Cardelús & Chazdon, 2005; Cervantes *et al.*, 2005; Sillett & Van Pelt, 2007). Access to the canopy of the tallest trees in the world was necessary for measurement of leaf water potential at various heights in giant redwoods, *Sequoia sempervirens*, in order to ascertain that maximum tree height, based on hydraulic conductivity, was 120–130 m (Koch *et al.*, 2004).

Distribution of foliage and foliage properties are primary aspects of forest structure that affect requirements for water and nutrients and rates of photosynthesis, evapotranspiration, net gas exchange, and interception of precipitation, particulates and aerosols (Gutschick, 1984; Ellsworth & Reich, 1993; Harley *et al.*, 1996; Dominy *et al.*, 2003; Fyllas *et al.*, 2009; Asner & Martin, 2011). Canopy foliage is composed of different tree species, which differ in size, shape and various chemical components, and different configurations and chemical composition within trees, based on availability of light, water and nutrients, as well as foliage of associated epiphytes (Ellsworth & Reich, 1993; Dominy *et al.*, 2003; Fyllas *et al.*, 2009; Asner & Martin, 2011).

Obvious differences in foliage distribution arise from variation in leaf size, shape, thickness and within-branch density among tree species, for example, between conifers, with dense needle-shaped foliage, and broad-leaved angiosperms; among broad-leaved species with simple vs compound leaves; and between deciduous trees, with foliage only during the growing season, and evergreens, which retain foliage year-round and often for several years. Foliage size, shape, thickness and density represent important tradeoffs among photosynthetic efficiency, energy and nutrient investment, and ease of replacement (Gutschick & Wiegel, 1988; Gutschick, 1999). Deciduous trees typically retrieve nutrients, especially nitrogen, before senescence (Marschner, 1995), resulting in different qualities of litterfall contributing to canopy–forest floor interaction.

The arrangement of leaves along the three-dimensional branch architecture also varies among tree species and reflects specific adaptations to optimize photosynthetic efficiency. Trees with long-lived leaves that can maintain photosynthesis under diffuse light may retain leaves along branches (e.g. Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco), whereas trees with short-lived leaves or leaves that require full sun may retain only a cluster of leaves at the exposed ends of branches (e.g. *Cecropia* spp.). Leaf distribution and photosynthetic efficiency also reflect leaf angle relative to branch angle and direction of sunlight and the arrangement of tree crowns of various species in three-dimensional canopy space. Some crowns have denser foliage (higher leaf area index) than do others.

Relying on canopy access, Hietz & Hietz-Seifert (1995a,b) and Cardelús (2007) tackled the challenges of sampling epiphytes, creating standardized techniques with respect to temporal variability: short, intermediate and long-term sampling. Cardelús' short-term method involves a rapid technique to quantify species richness, and includes standardizing the number of branches as well as the area/branch sampling space. Species counts (presence/absence) per branch were analyzed using sample based rarefaction curves to determine if species saturation is reached (Cardelús *et al.*, 2006). Intermediate sampling methodology involved more extensive canopy data collection to include not only number of epiphytes but also abundance of each species along branch transects or within plots within a three-dimensional canopy space (Cardelús, 2007). Long-term sampling protocols involve methods for measuring species richness, abundance and distribution, as well as demography, whereby researchers return to permanent vertical transects in the canopy marked with permanent tags or flagging tape (e.g. Zotz, 2005).

Canopy access also facilitated more quantified and accurate estimates of arthropod diversity and distribution in whole forests (Basset *et al.*, 2007). The Biodiversity of Soil and Canopy Athropods (IBISCA) is an international research protocol developed by an international team of entomologists in response to the lack of large data sets on the diversity and distribution of arthropods at multiple scales in tropical forests (Leponce *et al.*, 2010). The IBISCA protocol includes multi-scale, multi-taxa, multi-methods, and many researchers and volunteers to collect and process the voluminous collections. IBISCA has set a new 'industry standard' of international collaboration and exhaustive baseline data for several tropical sites, with many specimens still under investigation and classification (Basset *et al.*, 2007). IBISCA has illustrated the importance of canopy sampling as well as seeking cost-efficient cataloguing and processing of biodiversity samples, still major hurdles for biodiversity inventories of whole forests. The jury is still out on the exact number of species on our planet (ranging from as low as 10 million to as high as 100 million), but access into whole forests inspired the significantly higher estimates of global species composition (May, 2010).

In the scientific literature published before canopy access, herbivory was usually measured by simplified methods of sampling leaves from understory to mid-canopy. Most estimates indicated *c.* 5–8% leaf area eaten, based on leaves collected at a point in time (aka, a snapshot), often from low-hanging branches or picked up from the forest floor (e.g. Bray & Gorham, 1964; Odum & Ruiz-Reyes, 1970; Schowalter *et al.*, 1981; Landsberg & Ohmart, 1989). In 1979, Lowman not only used SRTs to monitor whole-tree herbivory, but she also executed monthly monitoring observations to record the amount defoliated from individual leaves over their entire life span. This whole-tree approach led to a two- or three-fold increase in estimates of the amount of foliage consumed by herbivores (mostly arthropods in the case of Australian rain forests) (Lowman, 1984, 1985). Similar corrections were made for Australian dry forests (Lowman & Heatwole, 1992), and neotropical forest canopies (Lowman, 2009b). Measuring whole-forest herbivory not only required canopy access for accuracy, but also relied upon careful attention to vertical changes in temporal and spatial factors including individual leaves, branches, height above ground, crowns, forest stands, and types of forest (Lowman, 1985).

As a result of access into canopies of 800-yr-old, 70-m-tall conifers on Vancouver Island, Canada, Winchester (2006) discovered that perched soils harbored a diverse assemblage of oribatid mites adapted to their arboreal environment and largely distinct from the more familiar assemblages of oribatids associated with litter decomposition on the forest floor. Similarly, Erwin's initial fogging surveys of neotropical trees led to his extrapolation that there may be over 30 million species on the planet, not the 1–2 million as was previously estimated (Erwin, 1982).

Although not part of the within-canopy access toolkit, remote sensing was an important development that advanced canopy research. Aerial photography pioneered the notion of quantifying volume of timber, conditions of forest stands, and even the shapes of individual crowns (e.g. Aldrich & Drooz, 1967). More recently, satellite imagery, such as provided by Lidar and digital photography, can facilitate mapping of tree crowns, diversity of stands, discrimination of tree crowns and lianas, and even distribution of populations over entire regions (Castro-Esau *et al.*, 2004; Sánchez-Azofeifa & Castro-Esau, 2006; Kalacska *et al.*, 2007; Palace *et al.*, 2008). With larger budgets, multi-sensor airborne sensor platforms such as Lidar can provide information about canopy structure (Asner *et al.*, 2008), condition (Carter & Knapp, 2001) and chemical composition of forest canopies (Asner & Vitousek, 2005). Combined with some degree of ground-confirmation and intensive data collection in the understory, these images enable a detailed analysis of the whole forest, although these technologies remain beyond the reach of most individual researchers at this point in time.

IV. Canopy communities – their inhabitants, environment, and processes

1. Canopy communities

Canopy access in the 1980s led to discoveries of communities of microorganisms, epiphytes and animals that mirror the diversity of canopy habitats and resources. These organisms can also modify canopy structure and canopy interaction with the atmosphere and forest floor. Various lichens, mosses, etc. form epiphytic mats (Nadkarni, 1984; Yanoviak *et al.*, 2007) on branches and boles. Epiphytes represent a major component of the photosynthetic and water-holding capacity of the canopy (Fig. 4) (Pypker *et al.*, 2005; Sillett & Van Pelt, 2007; Díaz *et al.*, 2010). Epiphytes also accumulate arboreal soil and litter and support development of the distinct communities associated with the arboreal soil/litter environment (Yanoviak *et al.*, 2007). Perched soils represent important reservoirs for seeds (seed bank) that may facilitate regeneration (Nadkarni & Haber, 2009). Some epiphytes, such as the birdnest ferns of tropical forests, reach large size on crotches or large branches that have sufficient soil accumulation and are capable of supporting fern weights up to 200 kg fresh weight apiece (Ellwood *et al.*, 2002). Increased weight of large epiphytes following heavy rains may cause breakage of smaller branches. These plants greatly increase habitat area for canopy fauna (Richardson *et al.*, 2000; Ellwood *et al.*, 2002) and for interception of airborne moisture and nutrients (see the last paragraph of section IV. 2).

Plant parasites and endophytes are important components of forest canopies (Carroll, 1988; Shaw *et al.*, 2005). Parasites include those growing externally (e.g. mistletoes, fungi, and

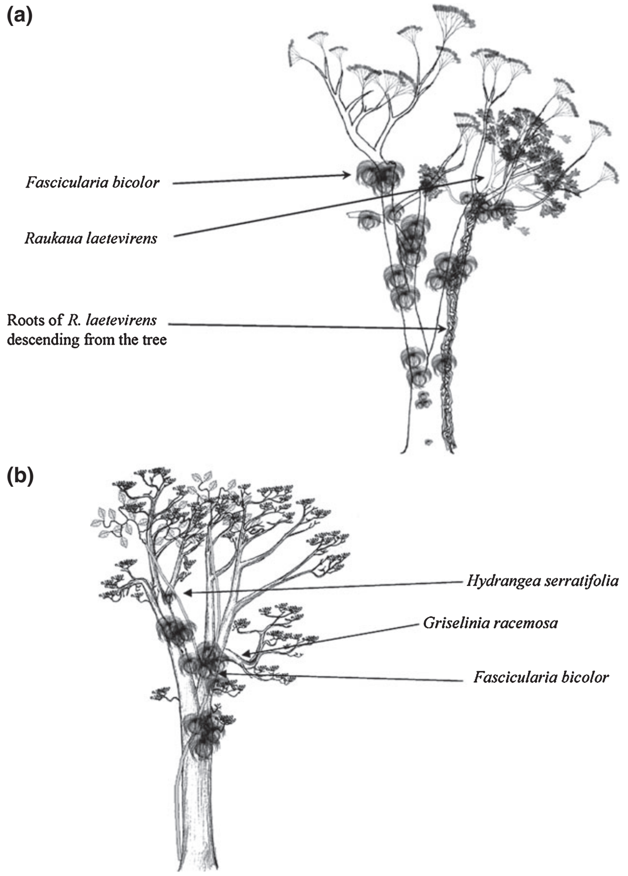

Fig. 4 Distribution of epiphyte size classes in canopies of two emergent trees (a and b) in temperate old-growth rain forest in Chile. From Díaz *et al.* (2010) with permission from Elsevier.

strangler figs) as well as those growing internally, often indistinguishable from endophytes (Moffett, 2000). Both groups affect canopy condition by removing nutrients, providing additional resources, and contributing chemicals that aid in defense of the host plant (Carroll, 1988).

Canopy animals represent a diverse and important component of canopy communities. Invertebrates and birds are diverse and functionally important treetop components in both temperate and tropical forests, whereas amphibians, reptiles and mammals are more diverse and important in tropical forests. Although invertebrate diversity mirrors tree species diversity and environmental conditions (e.g. Erwin, 1982; Novotný *et al.*, 2002, 2006; Gering *et al.*, 2007), most tree crowns host dozens to hundreds of species that represent specialized and generalized herbivores (including folivorous and sap-sucking species), detritivores, predators and parasites (Schowalter & Ganio, 2003). The small size and heterothermy of these organisms make them particularly sensitive to vertical gradients of temperature and relative humidity, as well as variation in resources. Many species (e.g. aphids, scale insects and leaf miners) are small enough to live within individual leaves or within the boundary layer of plant surfaces that have relatively constant temperature and moisture conditions. Even smaller, tardigrades may be common in forest canopies, but very few surveys exist (see Miller, 2004).

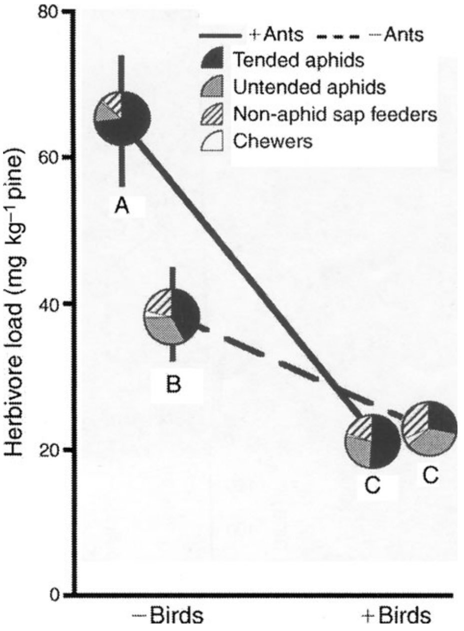

Fig. 5 Effects of bird and/or ant exclusion on total herbivore density and composition (pie charts) in ponderosa pine, *Pinus ponderosa* Douglas ex Lawson, canopies. Herbivore densities (means ± SE) are for six post-treatment months. Means with different letters differ significantly ($P < 0.05$). The interaction between bird and ant effects was significant ($P = 0.03$). From Mooney (2007) with permission from the Ecological Society of America.

Some animal groups are associated exclusively with specific canopy habitats. Epiphyte mats and accumulated soil host rich assemblages of specialized arthropods (Yanoviak *et al.*, 2007). Other arthropods occupy the aquatic environments of treeholes (Yanoviak, 1999) or epiphytes (Richardson *et al.*, 2000). Vertebrates may live and nest in forest canopies (e.g. tree frogs, birds, squirrels and monkeys), whereas some species forage in tree canopies (e.g. snakes, hunting cats, and bats) (Reagan & Waide, 1996; Kays & Allison, 2001; Malcolm, 2004). Increasingly, canopy dwellers show sensitivity to changes in landscape composition, especially forest fragmentation that interrupts large-scale movement among suitable habitat patches (Whelan, 2001; Anzures-Dadda & Manson, 2007; Arriaga-Weiss *et al.*, 2008; Baker & Olubode, 2008; Stouffer *et al.*, 2009).

Interactions among species affect community structure and consequences for canopy processes. For example, predaceous birds vs ants alter canopy herbivore abundances in different ways that affect canopy productivity (Fig. 5) (Marquis & Whelan, 1994; Terborgh *et al.*, 2001; Mooney, 2007). Animals may form or modify structures in canopies as a result of nest-building or other activities. Woodpeckers and other birds excavate cavities in branches and boles that can be used by other animals or eventually fill with water or debris to provide new habitats. Bees, ants and termites construct arboreal nests from sediments and/or organic matter, thereby increasing the complexity of canopy structure.

2. Canopy–atmosphere interaction

Forest canopies provide a large surface area of branches and foliage for interception of solar heat, precipitation and airflow.

Canopy height, canopy cover and vegetation type determine how much shade is provided and precipitation and wind are intercepted before reaching the forest floor (Monteith, 1973; Gutschick, 1999; Juang *et al.*, 2007). Photosynthesis by the forest canopy is the process that stores energy fixed from atmospheric carbon dioxide in carbohydrates and drives whole-forest functions, as well as ecosystem services valued by humans. Respiration reverses this process as the energy of stored carbohydrates is released to perform the various metabolic functions of trees and the community of organisms in the canopy. Fluxes of these and other biogenic gases affect carbon storage and distribution in the canopy and, in turn, influence atmospheric conditions regionally and globally (Lerdau & Throop, 1999; Turner *et al.*, 2005, 2007; Misson *et al.*, 2007).

Taller, denser canopies ameliorate solar heating and significantly reduce temperatures within and below the canopy (Fig. 6) (Foley *et al.*, 2003; Madigosky, 2004; Juang *et al.*, 2007). The forest canopy absorbs solar energy and reflects light and heat, lowering albedo and reducing surface temperatures (Gash & Shuttleworth, 1991; Lewis, 1998; Foley *et al.*, 2003). Albedo is inversely related to canopy height and 'roughness' (the degree of unevenness in canopy surface), declining from 0.25 for canopies < 1 m in height to 0.10 for canopies > 30 m height, and reaches lowest values in tropical forests with very uneven canopy surface (Monteith, 1973). Canopy roughness also generates turbulence in airflow (Fig. 7) (Raupach *et al.*, 1996; Finnigan, 2000; Cassiani *et al.*, 2008; Su *et al.*, 2008), thereby contributing to surface cooling by wind (sensible heat loss), evapotranspiration (latent heat loss), and rise of moist air to altitudes at which condensation and precipitation occur (Meher-Homji, 1991; Foley *et al.*, 2003). At night, the canopy absorbs reradiated infrared energy from the ground, maintaining warmer nocturnal temperatures, compared with canopy gaps or deforested sites.

Canopies intercept fog or rising clouds, augmenting annual precipitation (Brauman *et al.*, 2010). Deeper and denser canopies intercept more precipitation than do shorter and sparser

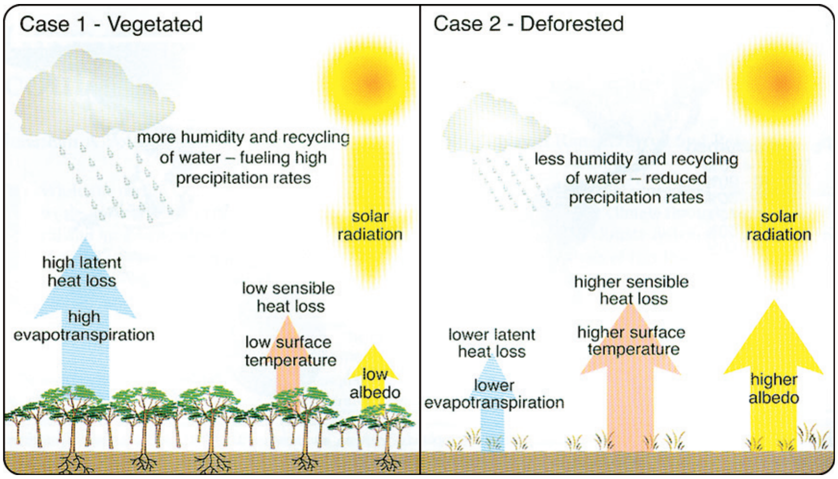

Fig. 6 Effects of forest canopies on climatic variables. From Foley *et al.* (2003) with permission from the Ecological Society of America.

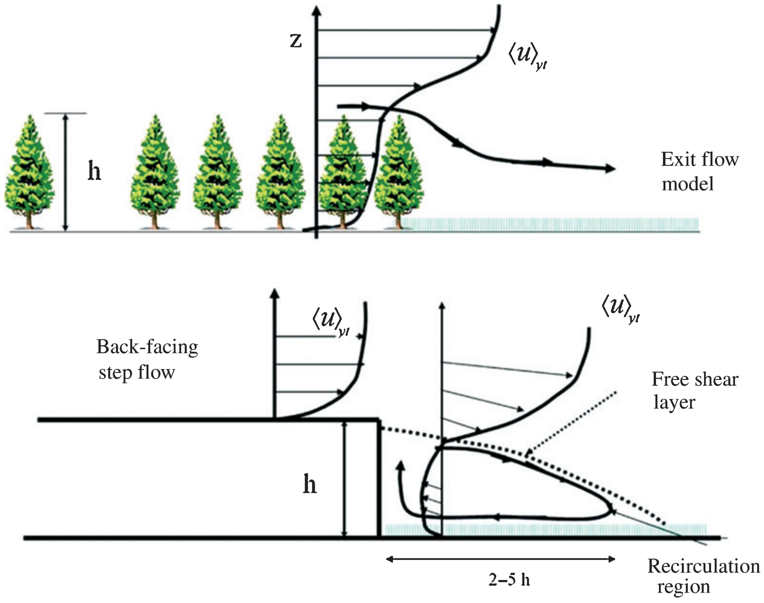

Fig. 7 Diagrammatic representation of two extremes in air flow over an edge between forest and clearing. At low foliage density or wind speed, relatively unimpeded air flow is described by an exit flow model (top). At higher foliage density or wind speed, impedance by the canopy is described by a back-facing step (BFS) flow model with a recirculation zone in the clearing where sinking airflow strikes the surface and another recirculation zone at the edge where the back-flow contacts the tall forest canopy. h, canopy height; u_{yt}, streamwise velociety; z, boundary layer height. From Cassiani *et al.* (2008) with permission from Springer.

canopies. Epiphytes increase water interception and storage (Pypker *et al.*, 2006). Dry deposition of particulate materials and nutrients often is a substantial proportion of total atmospheric inputs to forest canopies (Lovett & Lindberg, 1993). Interception of precipitation channels and stores water and dissolved nutrients in canopy reservoirs (such as tree holes and phytotelmata), and reduces the volume and impact of water reaching the forest floor, thereby reducing erosion and facilitating infiltration and storage in litter and soil.

Evapotranspiration contributes to canopy cooling and to convection-generated condensation above the canopy, thereby increasing local precipitation (Fig. 6) (Meher-Homji, 1991; Foley *et al.*, 2003; Juang *et al.*, 2007). Evapotranspiration increases relative humidity above the canopy and coupled with strong advective moisture flux, especially in the tropics, promotes local cloud formation (Trenberth, 1999). Furthermore, volatile chemicals emitted from canopy foliage can serve as precipitation nuclei (Facchini *et al.*, 1999). Canopy removal over large areas, that is, deforestation, has been associated with declining local and regional precipitation (Meher-Homji, 1991; Janssen *et al.*, 2008) as a result of positive feedback between reduced canopy cover, increased albedo and regional drying.

Forest canopies intercept airflow, reducing wind speed, creating turbulence (as described in the second paragraph of this section) and acquiring particles and aerosols from the air. Reduced airflow affects canopy gradients in temperature, relative humidity and, consequently, evapotranspiration rate. Dry deposition of particles (adsorption) and absorption of aerosols provide sediment and material that enhance canopy function (soil development and nutrient input) or stress plants and interfere with canopy function (pollutants). For example, Solberg *et al.* (2009) reported that European forests, especially pine and spruce forests, have shown greater-than-predicted growth rates over the past 15 yr, explained largely by a fertilization effect of atmospheric nitrogen deposition.

Forest canopies generate a number of volatile organic compounds (VOCs) that influence atmospheric chemistry, especially oxidative potential (Guenther *et al.*, 1996; Heald *et al.*, 2009; Lelieveld *et al.*, 2008). The most abundant VOCs are isoprene and monoterpenes (Lerdau *et al.*, 1997). Tropical forests are the largest source of isoprene (Lerdau & Throop, 1999; Lelieveld *et al.*, 2008). Isoprene biosynthesis and emission rates are related to light intensity, temperature and foliar nitrogen availability, whereas monoterpene biosynthesis and emission rates appear to be controlled primarily by temperature (Harley *et al.*, 1996, 1997; Lerdau *et al.*, 1997; Pressley *et al.*, 2006; Heald *et al.*, 2009). Methanol and acetone also are emitted by many plant species. Canopy foliage and their animal residents emit additional volatile compounds (e.g. plant signaling and defensive compounds and animal pheromones) that have relatively little effect on atmospheric conditions, but are critical to regulating species interactions (Cardé & Baker, 1984; Murlis *et al.*, 1992).

A major effect of these compounds is their light-sensitive oxidation into hydroxyl radicals, ozone, and carbon monoxide (Lerdau *et al.*, 1997; Lelieveld *et al.*, 2008; Heald *et al.*, 2009). Carbon monoxide, in particular, influences the oxidizing capacity of the atmosphere and is involved in photochemical reactions that increase atmospheric ozone concentration. However, isoprene also functions to increase the longevity of methane in the atmosphere, thereby indirectly contributing to global warming (Lerdau *et al.*, 1997; Lerdau & Throop, 1999; Heald *et al.*, 2009). Background isoprene emission by forests appears to be in balance with atmospheric oxidative capacity and may function to maintain atmospheric conditions conducive to forest production, but deforestation and conversion to agricultural or urban uses is likely to disrupt this balance (Lelieveld *et al.*, 2008).

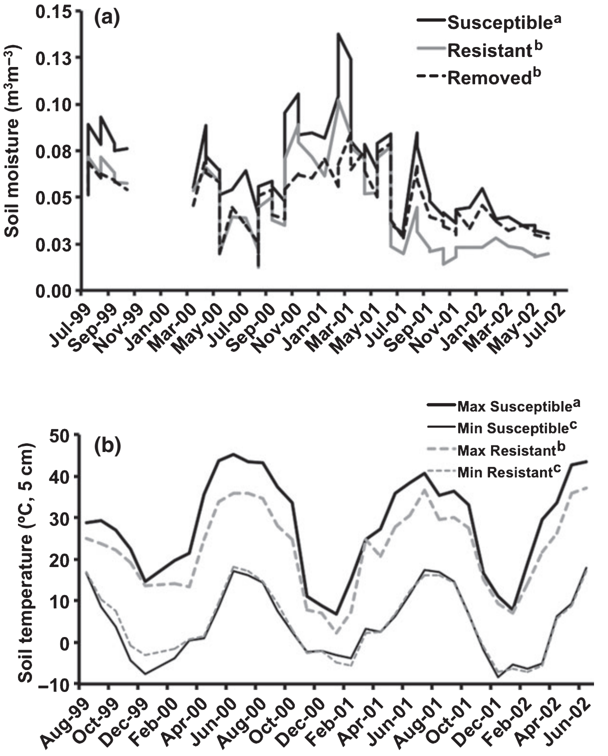

Fig. 8 Effect of herbivory by scale insects, *Matsucoccus acalyptus*, on soil moisture (a) and temperature (b) in a piñon-juniper (*Pinus edulis* Engelmann/ *Juniperus monosperma* Engelmann) woodland in northern Arizona during August 1999–June 2002. Treatments included trees that were susceptible or resistant to the scale or susceptible but with scales removed. Different letters indicate significant differences, using contrasts. From Classen *et al.* (2005) with permission from the Soil Science Society of America.

Associated canopy organisms can affect these canopy–atmosphere interactions in a number of ways. Epiphytes can contribute to canopy moderation of forest microclimate. Stuntz *et al.* (2002) found that epiphytes significantly reduced midday temperatures and evaporative drying in the surrounding canopy, even compared with branches within the same tree that were devoid of epiphytes. Classen *et al.* (2005) demonstrated that herbivory by both sap-sucking and folivorous insects reduced foliage density enough to reduce crown shading and interception of precipitation and affect temperature and relative humidity around treated trees enough to affect ecosystem processes (Fig. 8).

3. Canopy–forest floor interactions

Forest canopies significantly affect, and are affected by, conditions on the forest floor. Forest canopies intercept sunlight, reflecting heat and shading the forest floor, thereby reducing albedo and cooling the canopy and forest floor (Gash & Shuttleworth, 1991; Foley *et al.*, 2003; Janssen *et al.*, 2008). This insulating effect increases with canopy cover and canopy depth. The temperature at the forest floor under dense, complex canopies typically remains 2–4°C cooler than at the top of the canopy, with the difference between canopy surface and forest floor reaching a maximum of 10–12°C at midday when ambient temperature peaks and disappearing at night (Parker, 1995; Foley *et al.*, 2003; Madigosky, 2004). Litter falling from the canopy (see the sixth paragraph of this section) further insulates the soil surface from temperature extremes. As a result of this canopy cooling effect, temperatures at the forest floor are relatively constant diurnally and seasonally, providing stable conditions for a variety of organisms and processes.

Canopy opening as a result of disturbance, herbivory or deforestation reduces this shading effect (Classen *et al.*, 2005; see Fig. 8). Solar exposure can raise soil surface temperatures to 45°C during midday (Seastedt & Crossley, 1981), creating adverse conditions for many forest floor organisms that control decomposition and soil fertility (Amaranthus & Perry, 1987) and increasing evaporative loss of water. Furthermore, the effects of such soil warming can extend as much as 200 m into undisturbed forest, creating a horizontal gradient in forest floor temperature (Chen *et al.*, 1995). Loss of vegetation cover can initiate a positive feedback between evaporation and reduced precipitation that leads to further vegetation loss (Janssen *et al.*, 2008).

The canopy also intercepts and modifies precipitation, determining evapotranspiration rate (see the fourth paragraph of section IV. 2), throughfall and stemflow chemistry, droplet impact on the forest floor, and erosion (Foley *et al.*, 2003; Pypker *et al.*, 2005; Brauman *et al.*, 2010). Precipitation percolates through canopies with variable impacts to the forest floor (Ruangpanit, 1985; Meher-Homji, 1991). Interception rates increase with increasing canopy surface area and decreasing precipitation volume (Brauman *et al.*, 2010). Throughfall and stemflow show chemical enhancement, relative to raw precipitation, as a result of acquisition of nutrients from material adhered to or leached from foliage and branches during downward flow from the canopy. Foliage fragmentation resulting from herbivory or storm damage increases leaching from open edges of leaves (Kimmins, 1972; Seastedt *et al.*, 1983; Schowalter *et al.*, 1991). Increased nutrient content of throughfall increases flux of nutrients from canopy to forest floor. Water reaching the forest floor in excess of soil storage capacity leaches into streams and is exported from the forest.

Plants require water and nutrients for photosynthesis and canopy growth, and path-length resistance limits the height to which water can be drawn through capillaries, restricting maximum canopy height to 120–130 m (Koch *et al.*, 2004). If soil water becomes limiting, xylem cells cavitate, and the plant exhibits symptoms of drought stress (Mattson & Haack, 1987; Trumble *et al.*, 1993). Some bark beetles detect and use cell cavitation as a cue to water-stressed plants that are less able to produce defensive compounds and thereby become more suitable hosts (Mattson & Haack, 1987). If water limitation is severe, portions of the canopy die, leading to lateral branching, reiteration of trunks arising from the main trunk (Sillett & Van Pelt, 2007), and/or development of platforms that contribute unique habitats for various organisms.

Relative humidity at the forest floor typically is higher than at the top of the canopy, as a result of lower temperature and airflow, with the gradient particularly pronounced at midday (Parker, 1995; Madigosky, 2004). High relative humidity and low airflow minimize direct evaporation of soil moisture. However, when disturbance opens the canopy, soil exposure and warming increase the rate of evaporation and can lead to soil desiccation and/or flooding (Classen *et al.*, 2005; see Fig. 8). Counteracting this trend is the reduced interception of precipitation and uptake of soil water by the opened canopy, increasing soil moisture.

Biomass and nutrients are transferred from the canopy to the forest floor through several pathways. Carbohydrates produced in the canopy move downward through the phloem and are used for metabolic activity throughout the plant or are stored in woody tissues and roots. Allocation of net primary production to below-ground plant parts is often 50% or more in forests (Coleman *et al.*, 2004). Furthermore, 20–50% more carbon enters the rhizosphere from root exudates and exfoliates than is measured in root biomass at the end of the growing season (Coleman *et al.*, 2004). Root exudates support a variety of associated organisms, particularly nitrogen-fixing bacteria and mycorrhizal fungi that are critical to adequate uptake of water and nutrients by roots. Exudates also contribute to soil aggregate formation, a process that increases soil nutrient retention (Coleman *et al.*, 2004). Canopy materials rain to the forest floor as litterfall, affecting whole-forest dynamics. The degree of canopy shading and amount of throughfall govern litter temperature and moisture, two factors that control decomposition and respiration rates (Meentemeyer, 1978; Whitford *et al.*, 1981; Seastedt, 1984; Prescott, 2002). Decomposition rate also is a function of litter quality, as determined by tree species and litter material, for example, foliage vs wood (Prescott, 2002; Fonte & Schowalter, 2004).

Canopy organisms can substantially affect canopy–forest floor interactions. Epiphytes added 140 kg per tree in a temperate rain forest in Chile (Díaz *et al.*, 2010) and added additional mass when filled with water. Breakage of over-weighted branches during storms is common. A number of insects have life cycles that are divided between canopy and forest floor habitats. Some folivores feed on canopy resources during immature stages and pupate on the forest floor (e.g. Selman & Lowman, 1984; Miller & Wagner, 1984). Others feed on below-ground tissues during immature stages but emerge and affect canopy structure as adults, for example, cicadas, which can cause substantial twig and foliage loss during oviposition in twigs. Insect outbreaks add substantial amounts of relatively nutrient-rich animal tissues, fecal material, and green foliage fragments, as well as nutrient-enhanced throughfall to the forest floor (Grace, 1986; Hollinger, 1986; Frost & Hunter, 2004, 2007, 2008). These materials stimulate decomposition and mineralization on the forest floor (Fig. 9) (Seastedt & Tate, 1981; Schowalter & Crossley, 1983; Schowalter *et al.*, 1991, 2011; Frost & Hunter, 2004, 2007, 2008; Fonte & Schowalter, 2005). Roosting birds and bats can break branches

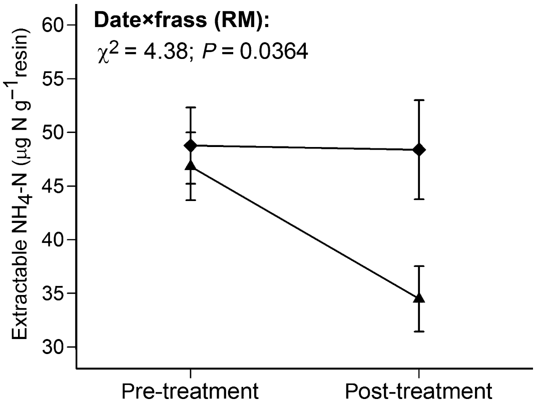

Fig. 9 Soil NH_4-N concentrations with (diamonds) or without (triangles) added insect frass, as estimated by ion-exchange resin bags. Data are means ± 1 SE (n = 60). RM indicates that data were analyzed as nonparametric repeated measures. From Frost & Hunter (2004) with permission from the Ecological Society of America.

and add feces that enrich soils below rookeries. Some forest-floor animals (e.g. elephants) can reach and substantially influence canopy structure and function up to 4–5 m height, and canopy detritivores contribute to decomposition *in situ* before material reaches the forest floor (Fagan *et al.*, 2006; Lindo & Winchester, 2007; Cardelús, 2010).

V. The role of forest canopies in providing ecosystem services

Many canopy processes provide essential ecosystem services on which human beings depend for survival. Forest ecosystem services are linked directly to the canopy by photosynthesis. In addition, canopy cover and interception of precipitation percolating through the canopy directly affect water flux and storage in the forest floor. In Guanxi, China seven surrounding regions paid Jinxiu County for water and soil conservation provided from its forests. Despite a lack of scientific literacy or extensive data sets, these people realized that forests mitigate floods, conserve fresh water, augment soil quality, and provide socio-economic benefits by ameliorating any hydrological extremes. Similarly, countries are increasingly aware that forest canopies regulate Earth's climate by controlling greenhouse gas exchange such as carbon dioxide. Forest ecosystems store approximately four times more carbon than found in the atmosphere, whereas tropical deforestation caused almost one-quarter of the globe's total greenhouse gas emissions in the 1990s (reviewed in Conte *et al.*, 2011). Models to predict whole-forest changes require information about forest canopies, as well as understory and below-ground components.

In the Amazon, plants produce chemical defenses against insect attack, and these chemicals, in turn, are sources of medicines, used by indigenous people as well as by pharmaceutical companies (Helson *et al.*, 2009). Other important ecosystem services include foods, construction materials, genetic libraries, gas exchange, carbon storage, fresh water conservation and circulation, and productivity as the basis of many food chains (reviewed in Lowman, 2009a; Schowalter, 2012; White *et al.*, 2010). Both timber and nontimber forest products play a key role in the economy of many countries, and require careful management to ensure sustainability (Nelson *et al.*, 2011).

These are some of the many reasons why we should worry about modifying or destroying tropical (or other) forests. When these providers of global services are altered, the changes that occur may have repercussions on a global scale (Lewis *et al.*, 2009). Conservation of tropical forests, including their diverse and productive canopy regions, is a relatively straightforward proposition; and the effects of reducing, modifying, and removing forests are not only well understood, but hundreds of scientific studies have measured and modeled the consequences of deforestation (reviewed in Laurance & Peres, 2006). Despite the direct links between ecosystem services and healthy forests (e.g. Vittor *et al.*, 2006), new solutions are required – hence the notions of recruiting diverse stakeholders to the decision-making table, or utilizing innovative conservation 'hooks' as described in the next section.

VI. Using canopy science as a 'hook' to inspire forest conservation

Since researchers first ascended in the 1970s into the upper reaches of forest and expanded their research into whole forests, millions of hectares of tropical rain forests have disappeared, along with thousands of undiscovered species. Similar loss has occurred in temperate forests, some with happy endings via reforestation, but often without the integrity and complexity of the original canopies. Changes in forest cover affect regional and global climate (Raupach *et al.*, 1996; Finnigan, 2000; Foley *et al.*, 2003; Juang *et al.*, 2007; Janssen *et al.*, 2008). Loss of forest canopies and consequences for ecosystem services are critical issues for subsequent generations. The next decade is critical. New ways to inspire forest conservation are urgently needed, in order to retain forest canopies as essential components of healthy ecosystems that in turn translate into sound economics.

One 'low-hanging fruit' is the maintenance of ecosystem services in secondary, or restored forests. While they may not have the complexity of primary forests, secondary forests nonetheless can support diverse floras and faunas (Chazdon, 2008; Dent & Wright, 2009) including native seed sources, pollinators, sustainable harvests, and productivity that in turn drives other ecosystem services, such as water quality (Uriarte *et al.*, 2011; Yackulic *et al.*, 2011). Farmers represent an emerging group of stakeholders working to restore secondary forest canopies. Eighteen countries in Africa are currently engaged in trials of fertilizer trees as part of a new agroforestry movement, 'evergreen agriculture' (Garrity *et al.*, 2010). Canopy foliage provides shade and litterfall nutrients for crops grown beneath. During her lifetime, Wangari Matthai oversaw the planting of millions of trees in her home country of Kenya.

These African countries may learn from the experience of Australia, which suffered widespread social and economic problems when forest diebacks ravaged rural landscapes in the late 20th Century (Lowman & Heatwole, 1992). In this case, over-clearing for sheep and cattle grazing, plus the accompanying loss of insectivorous birds, led to outbreaks of herbivorous beetles that defoliated and ultimately destroyed the remaining trees and their canopies. A program called 'a billion trees by 2000' was initiated, one farm at a time (Heatwole & Lowman, 1987). In Brazilian Amazonia, human modifications have led to significant increases in the fire regimes of secondary and disturbed forests, sometimes as much as 42% higher fire frequency (Aragao & Shimabukuro, 2010). Restoring degraded forests may require the suppression of some human activities, and even outright government intervention for successful restoration of healthy canopies.

Despite cautious optimism about the ecosystem services provided by secondary forests, the conservation of primary forests has become an increasing priority for most countries. Conventional stakeholders of many tropical forests are large government and conservation nongovernmental organizations, but the increasing decline of forests necessitates wider engagement by diverse stakeholders (reviewed in Lowman, 2009a). Use of forest canopies for cultural or ecotourism ventures may offer some reversal of regional deforestation: canopies provide an important cultural value, recreational activities that link to economic benefits, and a unique 'hook' that may inspire conservation of the whole forest.

Religious leaders represent an important, yet under-utilized, group of stakeholders in forest conservation. Sustainable land use practices and religious stewardship share similar conservation values (reviewed in Verschuuren *et al.*, 2010). One notable case is the Coptic or Christian Orthodox church in Ethiopia, where churchyards protect the last remaining tracts of native forests (Wassie-Eshete, 2007; Wassie *et al.*, 2009; Lowman, 2011) (Fig. 10). These church forest patches provide sanctuary for native trees and other biodiversity, soil and fresh water conservation, pollinators, and a vital cultural and spiritual heritage (Bossert *et al.*, 2006). Religious leaders are currently working with conservation biologists to educate local people about the ecosystem services of these remaining church forests, in particular the links between forests and fresh water, insect pollinators, honey, and shade (Lowman, 2011). Northeastern Ethiopia has lost over 95% of its forest cover, so the partnership between religion and science has the capacity to save the remaining 5% (Bongers *et al.*, 2006).

A final example of diverse stakeholders fostering forest conservation involves ecotourism as a source of sustainable income. When canopy researchers share their canopy access tools, the outcome can provide an economic incentive for local communities to conserve their forests rather than harvest them. In many tropical regions, the payments derived from harvest operations usually exceed the economic benefits of leaving the forest intact (Novotný, 2010); but the harvest revenues represent tempting, short-term profits. Ecotourism operations – involving canopy walkways, bird watching, education-based nature tours, spas and holistic medicine – can lead to sustainable income streams for local communities. Currently, over 20 canopy walkways operate in tropical forests around the world, serving research as well as ecotourism (http://www.canopyaccess.com). Walkways range in cost from US \$100 to US \$3000 m^{-1} to construct, but they provide educational opportunities to teach visitors about forest conservation, in addition to sustainable income (Lowman, 2009b). In the Sucasari tributary of the Rio Napo in Peru, the world's longest canopy walkway provides employment for > 100 local families, as well as education for thousands of visitors each year (Lowman, 2009b) (Fig. 11). Similar success stories exist for walkways in Western Samoa, Ecuador, and Gabon. At many sites, the benefits are less transparent, simply because Western accounting measures are not employed; but the conservation success is evident (Lowman, 2009b). In other cases, social media have leveraged diverse forest conservation stakeholders, including rock bands, clothing companies, school children, and Hollywood (see http://www.treefoundation.org).

VII. Conclusions – 'black boxes' in canopy science that remain

Currently, over half of the world's forests have been cleared, burned or harvested. In some countries such as Ethiopia and Madagascar, < 5% of the original forests remains, while 95%

Fig. 10 Coptic Orthodox priests are stewards of northeastern Ethiopia's last remaining forest patches, which provide essential ecosystem services to local communities.

Fig. 11 The world's longest canopy walkway, near the Sucasari tributary of the Rio Napo, Peru, provides employment for over 100 local families through ecotourism.

remains in Surinam and Guyana. This disparate approach to forest conservation, coupled with our knowledge that forests represent a critical global resource, indicates that treetops are at significant risk over the next few decades.

In addition to the over-arching conservation priorities, forest canopies represent a hot-spot for cutting-edge research. Canopy science still needs improved scaling of data from leaf to crown to canopy from local to global scales; demystifying of critical pathways that link transport of water and nutrients to and from the canopy via roots, branches, and bole; improved remote-sensing capabilities to distinguish effects of natural vs anthropogenic stressors on canopy health; expanded research on effects of interactions among canopy biodiversity and processes including herbivory, throughfall, net primary productivity (NPP), canopy–atmosphere interactions, and canopy–forest floor interactions; and an expanded network of towers and sensors to verify on site data from remote sensing. Unanswered questions to be addressed by future research include:

- How many species exist in tropical forest canopies, and what complex interactions of species are currently threatened by deforestation?
- What specific interactions between canopy biodiversity and processes serve as critical drivers for forest health? What is the prognosis for the continued health of these interactions?
- What factors accelerate forest canopy restoration? How will events such as insect outbreaks and warming temperatures impact the health of existing forests?
- How do canopies respond to climate change and what factors might buffer them from irreversible degradation?
- What types of forest canopies are at greatest risk from environmental changes, and how can we ameliorate their degradation? What are accurate assessments of forest canopy loss in different geographical regions?
- Can we predict how canopy processes affect ecosystem services such as water filtration and fresh water conservation, pollination, and food supplies, and the consequences of canopy removal, in various regions? Can metrics be created to allow accurate accounting of these values by local and regional governments?
- How do forest canopies affect human health?
- How can we educate the public, especially policy-makers, about the importance of conserving forest canopies and their inhabitants?

Acknowledgements

For one of us (M.L.), research in forest canopies was inspired by walking in the footsteps of Tansley as an MSc student in ecology at the University of Aberdeen, Scotland. In the classroom, Dr Charles Gimmingham spoke in glowing terms about Tansley's work, and our MSc class ventured into the heathlands to see first-hand some of the vegetation representing Tansley's legacy. My advisor, Peter Ashton, helped me construct a scaffold adjacent to stands of Scottish birch trees, to compare the understory versus canopy phenology of *Betula* species along elevational gradients. This was my inaugural canopy access experience, although those metal scaffolds were amazingly cold due to the frigid spring temperatures of Aberdeenshire. I went from chilly Scotland to the humid tropics of Queensland, Australia where the trees were too tall for scaffolding. In a moment of creative inspiration, I determined that the same equipment used by the Sydney University Spelunking club to descend into a cave might also propel me up into the tree canopy. For the other of us (T.S.), interest in canopy research was born from PhD research on effects of canopy fauna on biogeochemical cycling, under the direction of Dr Dac Crossley, who pioneered the use of branch bagging to assess canopy arthropod abundance and effect on canopy processes during the International Biological Programme. Since then, I have had the privilege of conducting canopy research in a variety of boreal, temperate and tropical forest ecosystems and evaluating the effects of natural and anthropogenic disturbances on canopy communities and processes. This paper is published with approval of the Director of the Louisiana Agricultural Experiment Station, as manuscript number 2012-234-6705. For these moments of inspiration (combined with the proverbial 99% perspiration), both of us are grateful to our global 'family' of canopy scientists, who shared risks to explore and seek to understand the eighth continent of the world: forest canopies.

References

Aldrich RC, Drooz AT. 1967. Estimated Frazer fir mortality and balsam woolly aphid infestation trend using aerial color photography. *Forest Science* **13**: 200–313.

Amaranthus MP, Perry DA. 1987. Effect of soil transfer on ectomycorrhiza formation and the survival and growth of conifer seedlings on old, nonreforested clear-cuts. *Canadian Journal of Forest Research* **17**: 944–950.

Andrade JL, Nobel PS. 1997. Microhabitats and water relations of epiphytic cacti and ferns in a lowland Neotropical forest. *Biotropica* **29**: 261–270.

Anzures-Dadda A, Manson RH. 2007. Patch- and landscape-scale effects on howler monkey distribution and abundance in rainforest fragments. *Animal Conservation* **10**: 69–76.

Appanah S, Chan HT. 1981. Thrips: pollinators of some dipterocarps. *Malaysian Forester* **44**: 234–252.

Arriaga-Weiss SL, Calmé S, Kampichler C. 2008. Bird communities in rainforest fragments: guild responses to habitat variables in Tabasco, Mexico. *Biodiversity Conservation* **17**: 173–190.

Asner GP, Hughes RF, Vitousek PM, Knapp DE, Kennedy-Bowdoin T, Boardman J, Martin RE, Eastwood M, Green RO. 2008. Invasive plants transform the three-dimensional structure of rain forests. *Proceedings of the National Academy of Sciences, USA* **105**: 4519–4523.

Asner GP, Martin RE. 2011. Canopy phylogenetic, chemical and spectral assembly in a lowland Amazonian forest. *New Phytologist* **189**: 999–1012.

Asner GP, Vitousek PM. 2005. Remote analysis of biological invasion and biogeochemical change. *Proceedings of the National Academy of Sciences, USA* **102**: 4383–4386.

Baker LR, Olubode OS. 2008. Correlates with the distribution and abundance of endangered Sclater's monkeys (*Cercopithecus sclateri*) in southern Nigeria. *African Journal of Ecology* **46**: 365–373.

Basset Y, Corbara B, Barrios H, Cuenoud PH, Leponce M, Aberlenc HP, Bail J, Bito D, Bridle JR, Castano-Meneses G *et al*. 2007. IBISCA-Panama, a large-scale study of arthropod beta-diversity and vertical stratification in a lowland rainforest: rationale, study sites and field protocols. *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Entomologie* **77**: 36–69.

Beebe W. 1949. *High jungle*. New York, NY, USA: Duell, Sloan and Pearce Publishers.

Bongers FA, Wassie A, Sterck FJ, Bekele T, Teketay D. 2006. Ecological restoration and church forests in northern Ethiopia. *Journal of the Drylands* **1**: 35–44.

Brauman KA, Freyberg DL, Daily GC. 2010. Forest structure influences on rainfall partitioning and cloud interception: a comparison of native forest sites in Kona, Hawai'i. *Agricultural & Forest Meteorology* **150**: 265–275.

Bray JR, Gorham E. 1964. Litter production in forests of the world. *Advances in Ecological Research* **2**: 101–157.

Cardé RT, Baker TC. 1984. Sexual communication with pheromones. In: Bell WJ, Cardé RT, eds. *Chemical ecology of insects*. London, UK: Chapman and Hall, 355–383.

Cardelús C, Colwell R, Watkins E. 2006. Vascular epiphyte distribution patterns: explaining the mid-elevation richness peak. *Journal of Ecology* **94**: 144–156.

Cardelús CL. 2007. Vascular epiphyte communities in the inner-crown of *Hyeronema alchorneoides* and *Lecythis ampla* at La Selva Biological Station, Costa Rica. *Biotropica* **39**: 171–176.

Cardelús CL. 2010. Litter decomposition within the canopy and forest floor of three tree species in a tropical lowland rain forest, Costa Rica. *Biotropica* **42**: 300–308.

Cardelús CL, Chazdon RL. 2005. Inner-crown microenvironments of two emergent tree species in a lowland wet forest. *Biotropica* **37**: 238–244.

Carroll G. 1988. Fungal endophytes in stems and leaves: from latent pathogen to mutualistic symbiont. *Ecology* **69**: 2–9.

Carter GA, Knapp AK. 2001. Leaf optical properties in higher plants: linking spectral characteristics to stress and chlorophyll concentration. *American Journal of Botany* **88**: 677–684.

Cassiani M, Katul GG, Albertson JD. 2008. The effects of canopy leaf area index on airflow across forest edges: large-eddy simulation and analytical results. *Boundary-layer Meteorology* **126**: 433–460.

Castro-Esau KL, Sánchez-Azofeifa GA, Caelli T. 2004. Discrimination of lianas and trees with leaf-level hyperspectral data. *Remote Sensing of Environment* **90**: 353–372.

Cervantes SE, Graham EA, Andrade JL. 2005. Light microhabitats, growth and photosynthesis of an epiphytic bromeliad in a tropical dry forest. *Plant Ecology* **179**: 107–118.

Chazdon RL. 2008. Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, **320**: 1458–1460.

Chen J, Franklin JF, Spies TA. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth Douglas-fir forests. *Ecological Applications* **5**: 74–86.

Classen AT, Hart SC, Whitham TG, Cobb NS, Koch GW. 2005. Insect infestations linked to changes in microclimate: important climate change implications. *Soil Science Society of America Journal* **69**: 2049–2057.

Coleman DC, Crossley DA Jr, Hendrix PF. 2004. *Fundamentals of soil ecology*, 2nd edn. San Diego, CA, USA: Elsevier/Academic Press.

Conte M, Nelson E, Carney K, Fissore C, Olwero N, Plantinga AJ, Stanley B, Rickets T. 2011. Terrestrial carbon sequestration and storage. In: Kareiva P, Tallis H, Ricketts TH, Daily GC, Polasky S, eds. *Natural capital*. Oxford, UK: Oxford University Press.

De Souza ALT, Martins RP. 2005. Foliage density of branches and distribution of plant-dwelling spiders. *Biotropica* **37**: 416–420.

Denison WC, Tracy DM, Rhoades FM, Sherwood M. 1972. Direct, non-destructive measurement of biomass and structure in living old-growth Douglas-fir. In: Franklin JF, Dempster LJ, Waring RH, eds. *Research on coniferous forest ecosystems*. Portland, OR, USA: Proc. Symp. Of Northwest Science Assoc., USDA Forest Serv., Pacific Northwest Exp. Stn, 147–158.

Dent DH, Wright SJ. 2009. The future of tropical species in secondary forests: a quantitative review. *Biological Conservation* **142**: 2833–2843.

Dial R, Bloodworth B, Lee A, Boyne P, Heys J. 2004. The distribution of free space and its relation to canopy composition at six forest sites. *Forest Science* **50**: 312–325.

Dial R, Roughgarden J. 1995. Experimental removal of insectivores from rain forest canopy: direct and indirect effects. *Ecology* **76**: 1821–1834.

Díaz IA, Sieving KE, Peña-Foxon ME, Larraín J, Armesto J. 2010. Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: a neglected functional component. *Forest Ecology & Management* **259**: 1490–1501.

Dominy NJ, Lucas PW, Wright SJ. 2003. Mechanics and chemistry of rain forest leaves: canopy and understory compared. *Journal of Experimental Botany* **54**: 2007–2014.

Ellsworth DS, Reich PB. 1993. Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**: 169–178.

Ellwood MDF, Jones DT, Foster WA. 2002. Canopy ferns in lowland dipterocarp forest support a prolific abundance of ants, termites, and other invertebrates. *Biotropica* **34**: 575–583.

Erwin TL. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *Coleopterists Bulletin* **36**: 74–75.

Facchini MC, Mircea M, Fuzzi S, Charlson RJ. 1999. Cloud albedo enhancement by surface-active organic solutes in growing droplets. *Nature* **401**: 257–259.

Fagan LL, Didham RK, Winchester NN, Behan-Pelletier V, Clayton M, Lindquist E, Ring RA. 2006. An experimental assessment of biodiversity and species turnover in terrestrial vs. canopy leaf litter. *Oecologia* **147**: 335–347.

Finnigan J. 2000. Turbulence in plant canopies. *Annual Review of Fluid Mechanics* **32**: 519–571.

Foley JA, Costa MH, Delire C, Ramankutty N, Snyder P. 2003. Green surprise? How terrestrial ecosystems could affect earth's climate *Frontiers in Ecology & the Environment* **1**: 38–44.

Fonte SJ, Schowalter TD. 2004. Decomposition of greenfall vs. senescent foliage in a tropical forest ecosystem in Puerto Rico. *Biotropica* **36**: 474–482.

Fonte SJ, Schowalter TD. 2005. The influence of a neotropical herbivore (*Lamponius portoricensis*) on nutrient cycling and soil processes. *Oecologia* **146**: 423–431.

Frost CJ, Hunter MD. 2004. Insect canopy herbivory and frass deposition affect soil nutrient dynamics and export in oak mesocosms. *Ecology* **85**: 3335–3347.

Frost CJ, Hunter MD. 2007. Recycling of nitrogen in herbivore feces: plant recovery, herbivore assimilation, soil retention, and leaching losses. *Oecologia* **151**: 42–53.

Frost CJ, Hunter MD. 2008. Insect herbivores and their frass affect *Quercus rubra* leaf quality and initial stages of subsequent decomposition. *Oikos* **117**: 13–22.

Fyllas N, Patiño S, Baker T, Bielefeld Nardoto G, Martinelli L, Quesada C, Paiva R, Schwarz M, Horna V, Mercado L *et al.* 2009. Basin-wide variations in foliar properties of Amazonian forest: phylogeny, soils and climate. *Biogeosciences* **6**: 2677–2708.

Garrity D, Akinnifesi F, Ajayi O, Weldesemayat S, Mowo J, Kalinganire A, Larwanou M, Bayala J. 2010. Evergreen agriculture: a robust approach to sustainable food security in Africa. *Food Security* **2**: 197–214.

Gash JHC, Shuttleworth WJ. 1991. Tropical deforestation: albedo and the surface-energy balance. *Climate Change* **19**: 123–133.

Gering JC, DeRennaux KA, Crist TO. 2007. Scale dependence of effective specialization: its analysis and implications for estimates of global insect species richness. *Diversity & Distributions* **13**: 115–125.

Grace JR. 1986. The influence of gypsy moth on the composition and nutrient content of litter fall in a Pennsylvania oak forest. *Forest Science* **32**: 855–870.

Guenther A, Greenberg J, Harley P, Helmig D, Klinger L, Vierling L, Zimmerman P, Geron C. 1996. Leaf, branch, stand and landscape scale measurements of volatile organic compound fluxes from U.S. woodlands. *Tree Physiology* **16**: 17–24.

Gutschick VP. 1984. Statistical penetration of diffuse light into vegetative canopies: effect on photosynthetic rate and utility for canopy measurement. *Agricultural Meteorology* **30**: 327–341.

Gutschick VP. 1999. Biotic and abiotic consequences of differences in leaf structure. *New Phytologist* **143**: 4–18.

Gutschick VP, Wiegel FW. 1988. Optimizing the canopy photosynthetic rate by patterns of investment in specific leaf mass. *American Naturalist* **132**: 67–86.

Haddow AJ, Corbet PS, Gilett JD. 1961. Studies from a high tower in Mpanga Forest, Uganda. *Transactions Royal Entomological Society of London* **113**: 249–368.

Hallé F, Pascal O, eds. 1990. *Biologie d'Une Canopée de Forêt Equatorial. II. Rapport de Missions: Radeau des Cimes Octobre/ Novembre 1991*. Cameroun: Reserve de Campo. Foundation Elf, Paris, France.

Harley P, Guenther A, Zimmerman P. 1996. Effects of light, temperature and canopy position on net photosynthesis and isoprene emission from sweetgum (*Liquidambar styraciflua*) leaves. *Tree Physiology* **16**: 25–32.

Harley P, Guenther A, Zimmerman P. 1997. Environmental controls over isoprene emission in deciduous oak canopies. *Tree Physiology* **17**: 705–714.

Heald CL, Wilkinson MJ, Monson RK, Alo CA, Wang G, Guenther A. 2009. Response of isoprene emission to ambient CO_2 changes and implications for global budgets. *Global Change Biology* **15**: 1127–1140.

Heatwole H, Lowman M. 1987. Dieback: death of an Australian landscape. In: Love R, ed. *If atoms could talk, search and serendipity in Australian science*. Richmone, Vic., Australia: Greenhouse Publications, 42–49.

Helson JE, Capson TL, Johns T, Aiello A, Windsor DM. 2009. Ecological and evolutionary bioprospecting: using aposematic insects as guides to rainforest plants active against disease. *Frontiers in Ecology & the Environment* **7**: 130–134.

Hietz P, Hietz-Seifert U. 1995a. Composition and ecology of vascular epiphyte communities along an altitudinal gradient in central Veracruz, Mexico. *Journal of Vegetation Science* **6**: 487–498.

Hietz P, Hietz-Seifert U. 1995b. Structure and ecology of epiphyte communities of a cloud forest in central Veracruz, Mexico. *Journal of Vegetation Science* **6**: 719–728.

Hollinger DY. 1986. Herbivory and the cycling of nitrogen and phosphorus in isolated California oak trees. *Oecologia* **70**: 291–297.

Janssen RHH, Meinders MBJ, van Nes EH, Scheffer M. 2008. Microscale vegetation–soil feedback boosts hysteresis in a regional vegetation–climate system. *Global Change Biology* **14**: 1104–1112.

Juang JY, Katul GG, Porporato A, Stoy PC, Sequeira MS, Detto M, Kim HS, Oren R. 2007. Eco-hydrological controls on summertime convective rainfall triggers. *Global Change Biology* **13**: 887–896.

Kalacska M, Bohman S, Sánchez-Azofeifa GA, Castro-Esau K, Caelli T. 2007. Hyperspectral discrimination of tropical dry forest lianas and trees: comparative data reduction approaches at the leaf and canopy levels. *Remote Sensing of Environment* **109**: 406–415.

Kays R, Allison A. 2001. Arboreal tropical forest vertebrates: current knowledge and research trends. *Plant Ecology* **153**: 109–120.

Kimmins JP. 1972. Relative contributions of leaching, litterfall, and defoliation by *Neodiprion sertifer* (Hymenoptera) to the removal of cesium-134 from red pine. *Oikos* **23**: 226–234.

Koch GW, Sillette SC, Jennings GM, Davis SD. 2004. The limits to tree height. *Nature* **28**: 851–854.

Landsberg J, Ohmart CP. 1989. Levels of defoliation in forests: patterns and concepts. *Trends in Ecology & Evolution* **4**: 96–100.

Laurance WF, Peres CA, eds. 2006. *Emerging threats to tropical forests*. Chicago, IL, USA: University of Chicago Press.

Lelieveld J, Butler TM, Crowley JN, Dillon TJ, Fischer H, Ganzeveld L, Harder H, Lawrence MG, Martinez M, Taraborrelli D *et al.* 2008. Atmospheric oxidation capacity sustained by a tropical forest. *Nature* **452**: 737–740.

Leponce M, Meyer C, Hauser C, Bouchet P, Delabie JHC, Weigt L, Basset Y. 2010. Challenges and solutions for planning and implementing large-scale biotic inventories. In: Eymann J, Degreeg J, Hauser CH, Monje JC, Van den Spiegel D, eds. *Manual on field recording techniques and protocols for all taxa biodiversity inventories. ABC taxa* **8**: 19–49.

Lerdau MT, Guenther A, Monson R. 1997. Plant production and emission of volatile organic compounds. *BioScience* **47**: 373–383.

Lerdau MT, Throop HL. 1999. Isopene emission and photosynthesis in a tropical forest canopy: implications for model development. *Ecological Applications* **9**: 1109–1117.

Lewis T. 1998. The effect of deforestation on ground surface temperatures. *Global & Planetary Change* **18**: 1–13.

Lewis SL, Lloyd J, Sitch S, Mitchard ETA, Laurance WF. 2009. Changing ecology of tropical forests: evidence and drivers. *Annual Review of Ecology, Evolution & Systematics* **40**: 529–549.

Lindo Z, Winchester NN. 2007. Oribatid mite communities and foliar litter decomposition in canopy suspended soils and forest floor habitats of western redcedar forests, Vancouver Island, Canada. *Soil Biology & Biochemistry* **39**: 2957–2966.

Louv R. 2011. *The nature principle*. Chapel Hill, NC, USA: Algonquin Books.

Lovett GM, Lindberg SE. 1993. Atmospheric deposition and canopy interactions of nitrogen in forests. *Canadian Journal of Forest Research* **23**: 1603–1616.

Lowman MD. 1984. An assessment of techniques for measuring herbivory: is rainforest defoliation more intense than we thought? *Biotropica* **16**: 264–268.

Lowman MD. 1985. Temporal and spatial variability in insect grazing of the canopies of five Australian rainforest tree species. *Australian Journal of Ecology* **10**: 7–24.

Lowman MD. 1999. *Life in the treetops – adventures of a woman in field biology*. New Haven, CT, USA: Yale University Press.

Lowman MD. 2004. Ecotourism and the treetops. In: Lowman MD, Rinker HB, eds. *Forest canopies*. San Diego, CA, USA: Elsevier, 475–485.

Lowman MD. 2009a. Biodiversity in tropical forest canopies as a "hook" for science education outreach and conservation. *Journal of Tropical Ecology* **50**: 125–136.

Lowman MD. 2009b. Canopy walkways for conservation: a tropical biologist's panacea or fuzzy metrics to justify ecotourism. *Biotropica* **41**: 545–548.

Lowman MD. 2011. Finding sanctuary – conserving the forests of Ethiopia, one church at a time. *The Explorers Journal* **4**: 22–27.

Lowman MD, Bouricius B. 1995. The construction of platforms and bridges for forest canopy access. *Selbyana* **16**: 179–184.

Lowman MD, Burgess E, Burgess J. 2006. *It's a jungle up there – more tales from the treetops*. New Haven, CT, USA: Yale University Press.

Lowman MD, Heatwole H. 1992. Spatial and temporal variability in defoliation of Australian *Eucalyptus*. *Ecology* 73: 129–142.

Lowman MD, Rinker HR, eds. 2004. *Forest canopies*. Oxford, UK: Elsevier.

Lowman MD, Schowalter T, Franklin JF. 2012. *Methods in forest canopy research*. Berkeley, CA, USA: University of California Press.

Lowman MD, Selman BJ. 1983. The biology and herbivory rates of *Novacastria nothofagi* Selman (Coleoptera: Chrysomelidae), a new genus and species on *Northofagus moorei* in Australian temperate rain forests. *Australian Journal of Zoology* 31: 179–191.

Madigosky SR. 2004. Tropical microclimatic considerations. In: Lowman MD, Rinker HB, eds. *Forest canopies*. San Diego, CA, USA: Elsevier, 24–48.

Malcolm JR. 2004. Ecology and conservation of canopy mammals. In: Lowman MD, Rinker HR, eds. *Forest canopies*. San Diego, CA, USA: Elsevier, 297–332.

Marquis RJ, Whelan CJ. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75: 2007–2014.

Marschner H. 1995. *The mineral nutrition of higher plants*, 2nd edn. San Diego, CA, USA: Academic Press.

Mattson WJ, Haack RA. 1987. The role of drought in outbreaks of plant-eating insects. *BioScience* 37: 110–118.

May R. 2010. Tropical arthropod species, more or less? *Science* 239: 41–42.

Meentemeyer V. 1978. Macroclimate and lignin control of litter decomposition rates. *Ecology* 59: 465–472.

Meher-Homji VM. 1991. Probable impact of deforestation on hydrological processes. *Climate Change* 19: 163–173.

Mehra PN, Bawa KS. 1968. B-Chromosomes in some Himalayan hardwoods. *Chromosoma* 25: 90–95.

Miller W. 2004. Tardigrades. In: Lowman MD, Rinker HB, eds. *Forest canopies*. San Diego, CA, USA: Elsevier, 251–258.

Miller KK, Wagner MR. 1984. Factors influencing pupal distribution of the pandora moth (Lepidoptera: Saturniidae) and their relationship to prescribed burning. *Environmental Entomology* 13: 430–431.

Misson L, Baldocchi DD, Black TA, Blanken PD, Brunet Y, Curiel Yuste J, Dorsey JR, Falk M, Granier A, Irvine MR *et al.* 2007. Partitioning forest carbon fluxes with overstory and understory eddy-covariance measurements: a synthesis based on FLUXNET data. *Agricultural & Forest Meteorology* **144**: 14–31.

Mitchell A. 1982. *Reaching the rainforest roof – a handbook on techniques of access and study in the canopy*. Leeds, UK: Leeds Philosophical & Literary Society.

Mitchell AW, Secoy K, Jackson T, eds. 2002. *The global canopy handbook*. Oxford, UK: Global Canopy Programme.

Moffett MW. 2000. What's "up"? A critical look at the basic terms of canopy biology. *Biotropica* 32: 569–596.

Monteith JL. 1973. *Principles of environmental physics*. New York, NY, USA: American Elsevier.

Mooney KA. 2007. Tritrophic effects of birds and ants on a canopy food web, tree growth, and phytochemistry. *Ecology* **88**: 2005–2014.

Murlis J, Elkinton JS, Cardé RT. 1992. Odor plumes and how insects use them. *Annual Review of Entomology* 37: 505–532.

Muul I, Liat LB. 1970. Vertical zonation in a tropical forest in Malaysia: methods of study. *Science* **196**: 788–789.

Nadkarni N. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. *Biotropica* **16**: 249–256.

Nadkarni NM, Haber WA. 2009. Canopy seed banks as time capsules of biodiversity in pasture-remnant tree crowns. *Conservation Biology* **23**: 1117–1126.

Nelson E, Montgomery C, Conte M, Polasky S. 2011. The provisioning value of timber and non-timber forest products. In: Kareiva P, Tallis H, Ricketts TH, Daily GC, Polasky S, eds. *Natural capital*. Oxford, UK: Oxford University Press, 129–149.

Novotný V. 2010. Rain forest conservation in a tribal world: why forest dwellers prefer loggers to conservationists. *Biotropica* 42: 546–549.

Novotný V, Basset Y, Miller SE, Weiblen GD, Bremer B, Cizek L, Drozd P. 2002. Low host specificity of herbivorous insects in a tropical forest. *Nature* **416**: 841–844.

Novotný V, Basset Y, Miller SE, Weiblen GD, Bremer B, Cizek L, Drozd P. 2003. *Arthropods of tropical forests*. Cambridge, UK: Cambridge University Press.

Novotný V, Drozd P, Miller SE, Kulfan M, Janda M, Basset Y, Weiblen GD. 2006. Why are there so many species of herbivorous insects in tropical rainforests. *Science* **313**: 1115–1118.

Odum HT, Ruiz-Reyes J. 1970. Holes in leaves and the grazing control mechanism. In: Odum HT, Pigeon RF, eds. *A tropical rain forest*. Springfield VA, USA: US Atomic Energy Commission, US Department of Commerce, 1–69 to 1–80.

Ozanne CMP, Anhuf D, Boulter SL, Keller M, Kitching RL, Kőrner C, Meinzer FC, Mitchell AW, Nakashizuka T, Silva Dias PL *et al.* 2003. Biodiversity meets the atmosphere: a global view of forest canopies. *Science* **301**: 183–186.

Palace M, Keller M, Asner GP, Hagen S, Braswell B. 2008. Amazon forest structure from IKONOS satellite data and the automated characterization of forest canopy properties. *Biotropica* **40**: 141–150.

Parker GG. 1995. Structure and microclimate of forest canopies. In: Lowman MD, Rinker HB, eds. *Forest canopies*. San Diego, CA, USA: Elsevier, 73–106.

Perrings CS, Naeem S, Ahrestana F, Bunker DE, Burkill P, Canziana G, Elmqvist T, Ferrati R, Fuhrman J, Jaksic F *et al.* 2010. Ecosystem services for 2020. *Science* **330**: 323–324.

Perry DR. 1986. *Life above the jungle floor*. New York, NY, USA: Simon & Schuster.

Prescott CE. 2002. The influence of the forest canopy on nutrient cycling. *Tree Physiology* **22**: 1193–1200.

Pressley S, Lamb B, Westberg H, Vogel C. 2006. Relationships among canopy level energy fluxes and isoprene flux derived from long-term, seasonal eddy covariance measurements over a hardwood forest. *Agricultural & Forest Meteorology* **136**: 188–202.

Pypker TG, Bond BJ, Link TE, Marks D, Unsworth MH. 2005. The importance of canopy structure in controlling the interception loss of rainfall: examples from a young and an old-growth Douglas-fir forest. *Agricultural & Forest Meterology* **130**: 113–129.

Pypker TG, Unsworth MH, Bond BJ. 2006. The role of epiphytes in rainfall interception by forests in the Pacific Northwest. I. Laboratory measurements of water storage. *Canadian Journal of Forest Research* **36**: 809–818.

Raupach MR, Finnigan JJ, Brunet Y. 1996. Coherent eddies and turbulence in vegetation canopies: the mixing-layer analogy. *Boundary-Layer Meteorology* **78**: 351–382.

Reagan DP, Waide RB, eds. 1996. *The food web of a tropical rain forest*. Chicago, IL, USA: University of Chicago Press.

Richardson BA, Richardson MJ, González G, Shiels AB, Srivastava DS. 2010. A canopy trimming experiment in Puerto Rico: the response of litter invertebrate communities to canopy loss and debris deposition in a tropical forest subject to hurricanes. *Ecosystems* **11**: 286–301.

Richardson BA, Rogers C, Richardson MJ. 2000. Nutrients, diversity, and community structure of two phytotelm systems in a lower montane forest, Puerto Rico. *Ecological Entomology* **25**: 348–356.

Ruangpanit N. 1985. Percent crown cover related to water and soil losses in mountainous forest in Thailand. In: El-Swaify SA, Moldenhauer WC, Lo A, eds. *Soil erosion and conservation*. Ankeny, IA, USA: Soil Conservation Society of America, 462–471.

Sale PF, ed. 2002. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. San Diego, CA, USA: Academic Press.

Sánchez-Azofeifa GA, Castro-Esau K. 2006. Canopy observations on the hyperspectral properties of a community of tropical dry forest lianas and their host trees. *International Journal of Remote Sensing* **27**: 2101–2109.

Schowalter TD. 2012. Insect herbivore effects on forest ecosystem services. *Journal of Sustainable Forestry*, in press.

Schowalter TD, Crossley DA Jr. 1983. Forest canopy arthropods as sodium, potassium, magnesium and calcium pools in forests. *Forest Ecology & Management* 7: 143–148.

Schowalter TD, Fonte SJ, Geaghan J, Wang J. 2011. Effects of manipulated herbivore inputs on nutrient flux and decomposition in a tropical rainforest in Puerto Rico. *Oecologia* **168**: 1141–1149.

Schowalter TD, Ganio LM. 2003. Diel, seasonal and disturbance-induced variation in invertebrate assemblages. In: Basset Y, Novotny V, Miller S, Kitching R, eds. *Arthropods of tropical forests*. Cambridge, UK: Cambridge University Press, 315–328.

Schowalter TD, Sabin TE, Stafford SG, Sexton JM. 1991. Phytophage effects on primary production, nutrient turnover, and litter decomposition of young Douglas-fir in western Oregon. *Forest Ecology & Management* 42: 229–243.

Schowalter TD, Webb JW, Crossley DA Jr. 1981. Community structure and nutrient content of canopy arthropods in clearcut and uncut forest ecosystems. *Ecology* 62: 1010–1019.

Seastedt TR. 1984. The role of microarthropods in decomposition and mineralization processes. *Annual Review of Entomology* 29: 25–46.

Seastedt TR, Crossley DA Jr. 1981. Microarthropod response following cable logging and clear-cutting in the southern Appalachians. *Ecology* **62**: 126–135.

Seastedt TR, Crossley DA Jr, Hargrove WW. 1983. The effects of low-level consumption by canopy arthropods on the growth and nutrient dynamics of black locust and red maple trees in the southern Appalachians. *Ecology* **64**: 1040–1048.

Seastedt TR, Tate CM. 1981. Decomposition rates and nutrient contents of arthropod remains in forest litter. *Ecology* **62**: 13–19.

Selman B, Lowman MD. 1983. The biology and herbivory rates of *Novacastria nothofagi* Selman (Coleoptera: Chrysomelidae), a new genus and species on *Nothofagus moorei* in Australian temperate rain forests. *Australian Journal of Ecology* **31**: 179–191.

Shaw DC, Chen J, Freeman EA, Braun DM. 2005. Spatial and population characteristics of dwarf mistletoe infected trees in an old-growth Douglas-fir – western hemlock forest. *Canadian Journal of Forest Research* **35**: 990–1001.

Shiels AB, Zimmerman JK, García-Montiel DC, Jonckheere I, Holm J, Horton D, Brokaw N. 2010. Plant responses to simulated hurricane impacts in a subtropical wet forest, Puerto Rico. *Journal of Ecology* **98**: 659–673.

Sillett SC, Van Pelt R. 2007. Trunk reiteration promotes epiphytes and water storage in an old-growth redwood forest canopy. *Ecological Monographs* **77**: 335–359.

Solberg S, Dobbertin M, Reinds GJ, Lange H, Andreassen K, Fernandez PG, Hildingsson A, de Vries W. 2009. Analysis of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: a stand growth approach. *Forest Ecology & Management* **258**: 1735–1750.

Stouffer PC, Naka LN, Strong C. 2009. Twenty years of understorey bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. *Diversity & Distributions* **15**: 88–97.

Stuntz S, Simon U, Zotz G. 2002. Rainforest air-conditioning: the moderating influence of epiphytes on the microclimate in tropical tree crowns. *International Journal of Biometeorology* **46**: 53–59.

Su HB, Schmid HP, Vogel CS, Curtis PS. 2008. Effects of canopy morphology and thermal stability on mean flow and turbulence statistics observed inside a mixed hardwood forest. *Agricultural & Forest Meteorology* **148**: 862–882.

Sutton SL. 2001. Alice grows up: canopy science in transition from wonderland to reality. In: Linsenmair KE, Davis AJ, Fiala B, Speight MR, eds. *Tropical forest canopies: ecology and management*. Netherlands: Kluwer Academic Publishers, 13–23.

Terborgh J, Lopez L, Nuñez VP, Rao M, Shahabuddin G, Orihuela G, Riveros M, Ascanio R, Adler GH, Lambert TD *et al.* 2001. Ecological meltdown in predator-free forest fragments. *Science* **294**: 1923–1926.

Trenberth KE. 1999. Atmospheric moisture recycling: role of advection and local evaporation. *Journal of Climate* **12**: 1368–1381.

Trumble JT, Kolodny-Hirsch DM, Ting IP. 1993. Plant compensation for arthropod herbivory. *Annual Review of Entomology* **38**: 93–119.

Turner DP, Ritts WD, Cohen WB, Maeirsperger TK, Gower ST, Kirschbaum AA, Running SW, Zhao M, Wofsy SC, Dunn AL *et al.* 2005. Site-level evaluation of satellite-based terrestrial gross primary production and net primary production monitoring. *Global Change Biology* **11**: 666–684.

Turner DP, Ritts WD, Law BE, Cohen WB, Yang Z, Hudiburg T, Campbell JL, Duane M. 2007. Scaling net ecosystem production and net biome production over a heterogeneous region in the western United States. *Biogeosciences* **4**: 597–612.

Uriarte M, Yackulic CB, Lim Y, Arce-Nazario JA. 2011. Influence of land use on water quality in a tropical landscape: a multi-scale analysis. *Landscape Ecology* **26**: 1151–1164.

Verschuuren B, Wild R, McNeely JA, Oviedo G. 2010. *Sacred natural sites – conserving nature and culture*. New York, NY, USA: Earthscan, IUCN.

Vittor AY, Gilman RH, Tielsch J, Glass G, Shields T, Lozano WS, Pinedo-Cancino V, Patz JA. 2006. The effect of deforestation on the human-biting rate of *Anopheles darlingi*, the primary vector of falciparum malaria in the Peruvian Amazon. *American Journal of Tropical Medicine & Hygiene* **74**: 3–11.

Wassie A, Sterck FJ, Teketay D, Bongers F. 2009. Tree regeneation in church forests of Ethiopia: effects of microsites and management. *Biotropica* **41**: 110–111.

Wassie-Eshete A. 2007. *Ethiopian church forests – opportunities and challenges for restoration*, PhD thesis. Wageningen Universiteit, the Netherlands.

Whelan CJ. 2001. Foliage structure influences foraging of insectivorous forest birds: an experimental study. *Ecology* **82**: 219–231.

White T, Asfaw B, Beyene Y, Haile-Selassie Y, Lovejoy CO, Suwa G, Wolde-Gabriel G. 2009. *Ardipithecus ramidus* and the paleobiology of Early Hominoids. *Science* **326**: 75–86.

Whitford WG, Meentemeyer V, Seastedt TR, Cromack K Jr, Crossley DA Jr, Santos P, Todd RL, Waide JB. 1981. Exceptions to the AET model: deserts and clear-cut forest. *Ecology* **62**: 275–277.

Wilson EO. 1992. *The diversity of life*. Boston, MA, USA: Harvard University Press.

Winchester NN. 2006. Ancient temperate rain forest research in British Columbia. *Canadian Entomologist* **138**: 72–83.

Yackulic CB, Fagan M, Jain M, Jina A, Lim Y, Marlier M, Muscarella R, Adame P, DeFries R, Uriarte M. 2011. Biophysical and socioeconomic factors associated with forest transitions at multiple temporal and spatial scales. *Ecology & Society* **16**: 15.

Yanoviak SP. 1999. Effects of leaf litter species on macroinvertebrate community properties and mosquito yield in Neotropical tree hole microcosms. *Oecologia* **120**: 147–155.

Yanoviak SP, Nadkarni NM, Solano JR. 2007. Arthropod assemblages in epiphyte mats of Costa Rican cloud forests. *Biotropica* **39**: 202–210.

Zotz G. 2005. Vascular epiphytes in the temperate zones – a review. *Plant Ecology* **176**: 173–183.